

NOTES ON THE WEST AUSTRALIAN PITCHER-  
PLANT (*CEPHALOTUS FOLLICULARIS*, LABILL.).

By A. G. HAMILTON.

(Plates i.-ii.)

This beautiful and extremely interesting pitcher-plant is found only near Albany, West Australia. During a visit to Albany in December, 1902, in company with Mr. C. R. P. Andrews, we searched for the plants to the eastward of the town towards the forts. We succeeded in finding a few stunted plants, and one very fine one, in a little gully running down to the beach. They grew among the long grass, almost in running water. This one specimen was the largest and most beautifully coloured that I saw. I then explored a heathy flat to the north-west of the town, but could not find any, till Mr. Andrews most obligingly guided me to a spot where it was very plentiful—a creek running parallel to the rifle-range, to the north of the town. Some yards away from the creek and on the western side, beyond the targets, there was a sloping bank of peaty soil, which was kept very sloppy by the soakage from the hill above, and here we found many of the plants, growing in little rosettes, but in the open, and on little elevations all round the bases of woody shrubs. Even at the season when I was there, which was in the middle of the dry time of the year, the ground was very wet. In the wet season it must be almost a running stream.

Judging from what I have read, and also heard from competent observers, of the plentifulness of the plants in former years, I think that in the locality I visited they are on the way to become extinct—the cause, so far as I could judge, being the trampling of stock feeding on the common. I had not the time to go farther afield, and so do not know if it is holding its own farther

out. But the very fact that it is restricted to one locality goes to show that it is a species in process of becoming extinct. I observed only one living, but quite a number of dead plants on the opposite bank of the creek, and here the ground was trampled bare by cattle.

In Kerner and Oliver's 'Natural History of Plants' (1), p. 130, *Cephalotus* is spoken of as coming from *Eastern Australia*, a mistake which has been made, or copied by other authors; and in Grant Allen's 'Story of the Plants' (2), p. 72, a *Sarracenia* is figured as "An Australian Pitcher Plant which eats insects." An excellent figure is given in Curtis' 'Botanical Magazine.' (3).

The plants are extremely attractive in appearance, both from the graceful shape and bright colouring of the pitchers. The prevailing colours are bright red to purplish-crimson, vivid green, and on the lids areolæ of translucent white. The plants growing in the open were much more brilliantly coloured than those in the shade. Indeed many of those in deep shade were without any red at all, the colours being light green and transparent patches. Pitchers which were dying off changed the green into yellow, and the crimson into orange-red, adding greatly to the variety of colour which a clump showed. The ordinary leaves, too, often assume bright crimson and yellow coloration when beginning to die.

At the time of my visit in mid-December, the plants were in very early bud, the flower-stalks being 10·2 to 20·4 cm. high; but the buds were so little advanced that the floral structure could not be made out even by dissection, and Mr. Andrews, who stayed some weeks longer than I did, informs me that up till the time of his leaving no flowers had opened. I was told by a resident that the flowers did not open till January and February. When the plants grew in the open, they were perfect rosettes, the pitchers on the outside, and the ordinary leaves (when there were any) in the centre. But there were not many of the latter, and for the most part they were small. I believe that the ordinary leaves develop in the autumn, reaching their full maturity in spring, and then gradually going off; while the

pitchers grow in winter and spring, and are fully formed and functional in summer, when the insects which they capture are most plentiful. They then probably die in autumn, and a fresh crop begins to grow in winter again. This was the case with plants which I have in cultivation, but a series of observations on the plants in their native habitat is needed to settle this and many other interesting points in their economy.

The pitchers vary much in size, independently of their age. Many of the mature pitchers were of small size.

The ordinary leaves are ovate, the length a little more than the breadth, narrowing into the petiole, which is about equal to the blade in the length. The average measurements are:—Total length 5 cm., breadth 1.8 cm. They are rather thick, and of a tough consistence when mature, and not grown in shade. The surface is very glossy in young leaves, less so in those which are mature. The margin is entire, and ornamented with a row of stiff hairs, white when young, and brownish in old leaves. Hairs of the same kind occur also on the wings and lids of the pitchers. Their peculiar structure will be alluded to later. Among the leaves we observed at Albany, my son discovered a very interesting monstrous form (fig. 1), and among the leaves on my cultivated plants several have appeared. These monstrosities are apparently common, as Professor Dickson has described and figured a series occurring in cultivated plants in the garden at Edinburgh University (4). There are stomata on the lower surface of the leaf, and small glands (to be described later) on both surfaces, rather more in number on the under than the upper side. In young leaves these pour forth quantities of some fluid which gives the leaves the varnished gloss they have, but I could not detect any sweet taste in the fluid. The stomata are of the ordinary character (fig. 2). I have been inclined to think that the small glands might be modified or altered stomata, but against this view there is the fact that they are found on the upper surface of the leaf, where there are no stomata. Glands of the same description occur on the inner and outer surface of both pitchers and lids, and are associated with stomata on the

outside of these. MacFarlane also found them "on the scales of young rhizomes; on the long, slender flower-stalks, and on the bracts which these bear. . . . On the outer surface of the sepals they are even more numerous and larger" (5). The epidermis cells in surface view are irregularly wavy, but less so on the under than the upper side (fig. 3). In section they are thin-walled and straight-sided, with a conical base. The mesophyll consists of rounded cells, with many air-spaces, and the palisade tissue on the upper surface is very slightly differentiated from the spongy tissue. The chlorophyll masses are fairly large, and in young leaves very brilliant green. Spiral conducting tissue, such as is usually associated with the carriage of water, is plentifully developed.

The pitchers (fig. 4) are roughly pitcher-shaped, but not symmetrical. They resemble the front part of a loose slipper. The petiole is attached below the junction of the lid and pitcher, and the veins spread palmately from the insertion. The lid is almost circular, and curved over the mouth. From the attachment of the lid four ribs run to the margin, the two centre ones forking so that at the edge there are six ribs, composed of thickish tissue. These ribs are green in young, purplish-red in mature pitchers. Between the ribs lies thin transparent tissue with no chlorophyll granules. These areolæ have a frosted appearance, like the similar tissue in the flowers of many species of *Pterostylis*, and similar areolæ are found in the pitchers of *Sarracenia* and *Darlingtonia*. The veins of the lid branch dichotomously at the base, and then form reticulations in the ribs. They pass through the areolæ transversely, but rarely fork there. On the ribs of the lid the stiff white hairs occur sparsely, and there is a fringe of the same hairs on the edge, some being quite double the length of others; they are white in young pitchers, rusty-brown in old ones. Besides these, short thick hairs with rounded heads, which stain with saffranin much more readily than the long ones, are found on the outside of the lid near its attachment (fig. 5). The interior of the lid is white or pinkish, with crimson streaks marking the situation of the ribs.

Dr. W. Woolls (5) says:—"In the pitcher-plant of Western Australia some of the leaves are converted into ovoid, or nearly globular pitchers, which have a lid attached to them. This lid is very irritable under certain conditions." I do not know what authority Dr. Woolls had for this statement, but as a matter of fact the lid is not irritable. In the very young state, the lid closes tightly over the orifice, and as it gets older, gradually opens, being most widely opened in mature pitchers, but there is no hinge, and it is only by using force sufficient to rupture the tissues of the attachment that it can be opened or closed more than in its natural state. Probably the mistake arose from seeing the lids in all degrees of openness in pitchers of various ages. Goebel, quoted by Strasburger (6), says the lid does not shut.

All round the orifice of the pitcher, from the base of the lid, there is a corrugated roll, the diameter being small near the lid, and thickest in the middle of the front aspect. The corrugations are produced internally in downward hooked teeth, 20 to 24 in number usually. The colour of the rim is red-brown to dark purplish-brown in mature specimens, and the surface is glossy. The texture is tough.

The pitchers have three projections or wings externally; one in front, beginning just under the corrugated rim, at the centre (fig. 4 *a*), narrow at first, and widening downwards towards the toe of the pitcher, when it suddenly narrows to a point. The wing consists of a narrow rib standing up at right angles to the pitcher surface, and on the upper edge spreading out into lateral free margins, so that a transverse section of it is like a broad-angled Y. These lateral expansions are thickly margined with the stiff, pointed hairs already mentioned, and these are found between the expansions in young pitchers, but are absent in mature ones, although the papillæ from which they rose can be seen with a hand lens. The other wings are lateral, beginning under the rim more than half-way back from the centre and running obliquely forwards and downwards (fig. 4 *b*), and terminate rather more than half-way down the pitcher, where

they narrow off to the surface, the lower end being just at the upper extremity of the lateral gland-mass of the interior. These lateral wings are thin ribs, widest at the upper end, and standing perpendicularly to the surface, but not extending laterally as the front wing does; they also have a border of stiff hairs.

As before said, the pitchers vary much in size when full grown. The largest, which I saw in our first search, I did not collect, or measure, but it was not less than 5.5 cm. long. The figure in Curtis' Botanical Magazine shows very large pitchers. The following are some measurements :—

LENGTH.		BREADTH.		DIAMETER OF ORIFICE.	
		Front to Back.	Side to Side.	Front to Back.	Transverse.
No. 1.	4 cm.	2.35 cm.	2.45 cm.	0.7 cm.	1.3 cm.
No. 2.	3.6 cm.	2.0 cm.	2.2 cm.	0.11 cm.	1.3 cm.
No. 3.	3.25 cm.	1.7 cm.	2.2 cm.	0.7 cm.	1.2 cm.

The coloration of the pitchers varies. Generally speaking, it consists of irregular markings of red or purplish on a green ground, and the general arrangement is similar to that in the pitchers of *Nepenthes*. The young pitchers are bright green. The outer surface is smooth but not glossy. The interior varies from green in very young pitchers, bright red in full grown specimens, and a deep glossy black in old ones. This when examined by transmitted light is a dark purplish-crimson. Young specimens in spirit bleach almost white, while older ones remain dark brown or blackish, the spirit becoming pink, which afterwards changes to dull brown. The deep colour of the interior, I think, depends on the amount of animal matter they contain, and I should not be surprised to learn that the exterior colouring has some relation to the same factor. This is a matter in which observations on the plant in its native habitat are required. When the pitchers are fading, the green parts turn yellow and the purple bright red.

The pitchers rest on the ground so that they slope forwards, throwing the surface line of the contained fluid higher up at the stalk end than in front, and it will be seen that this is related to the distribution of the internal glands.





The stiff hairs alluded to before are thus described by Professor Dickson (4) "Each is an elongated cell with pointed extremity, and a broad truncated base imbedded in a slightly elevated group of epidermis cells. This unicellular hair is solid from the tip to within  $\frac{1}{2}$  or  $\frac{1}{3}$  of the distance from the base. The cell cavity thus reduced is bounded by a distinct and highly refractive wall, and the *appearance* is thus produced of one cell encapsulated in another. According to the modern view of cell-thickening by interstitial intussusception, this would be a remarkable case of the differentiation of thickened cell-wall into two layers of different character. The hairs are minutely tuberculated on the outer surface." This is a very good description of these curious emergences, and needs little to be added. On the young pitchers the hairs are silvery-white (and almost as long as they are in older ones, so that they look like little vegetable porcupines), but when cleared with clove oil and examined under the microscope, there is a faint yellow coloration in the interior of the hair; and in older hairs it becomes a dark brown, sometimes quite opaque. In both old and young hairs the contents are granular. Altogether they bear a strong resemblance to those of some mammals. Some of them show one or more constrictions along their length (fig. 5 b). They are largest on the petioles and shortest on the wings. They are, as Prof. Dickson mentions, tuberculous on the external surface, but this can only be seen in dry and spirit-mounted specimens, the tubercles disappearing in clove oil or glycerin. The older hairs very often have the hyphæ of a fungus wound round them in spiral lines (fig. 5 c), and sometimes these penetrate to the cavity, in which case they grow straight up along the sides. I sent a slide to Mr. D. McAlpine, who was good enough to send me the following note:—" *Helminthosporum* spp. Hyphæ olivaceous, wavy, septate, not constricted at septa, branching,  $2\frac{1}{2}$ -3  $\mu$  broad, permeating cuticle and passing into hairs. Spores smoky-brown, 3-septate, constricted at septa, rounded at both ends, cylindric to fusiform, produced at the end of the branches,  $20-23 \times 4\frac{1}{2}-6 \mu$ , average  $22 \times 5 \mu$ ." It will be noticed in the figure that some of the spores are 4-septate.

The inner structure of the pitchers is simple. From beneath the incurved teeth of the rim, a thick ledge or collar, named by Prof. Dickson the conducting shelf, hangs down all round for a short distance—10-12 mm. It is produced clear of the pitcher walls, so that it forms an inner collar like that in a lobster-trap. The inner surface of the pitcher below this is very smooth and glossy, and with the lens, or even with the naked eye, this portion is seen to be full of small dots, which are glands similar to those found on all the exterior surface of the plant. They are most closely placed just round the insertion of the petiole, and extend downwards to the line of the top of the lateral gland mark at the sides, but lower in front. This downward limit is the highwater mark of the contained fluid, none occurring below (fig. 7). For this reason I am inclined to think that they are secretive and attractive in their nature. At any rate they are not likely to be absorptive. Prof. Dickson (4) points out that, unlike the glands of *Nepenthes*, they have no apparent connection with the vascular system. Thus the inner surface of the pitcher may be divided into the conducting shelf, the glandular, and the eglandular regions.

On each side, below the glandular surface, commencing at about the level of the lower extremity of the external lateral wing, and running obliquely downwards and forwards, is a slight elevation, called by Prof. Dickson the lateral coloured patch, but which I prefer to call the lateral gland mass (fig. 7 *glm*). These are kidney-shaped in outline, and with the naked eye small rounded projections from the surface are seen, most plentifully at the posterior margin, where also the substance of the mass is thickest. Examined with the hand lens, these are seen to be hemispherical elevations, and the microscope shows them to be glands of a larger size and more complete structure than those of the upper glandular region. In young pitchers the masses are lighter than the rest of the inner surface, but at length become purplish-red, the glands remaining yellowish. In fully matured pitchers, the masses are undistinguishable from the rest of the surface except by their rising above it, and by the lighter colour



of the glands. They are sometimes covered with a network of hyphæ, apparently of the same kind as those found on the hairs externally. Several of the main veins of the pitcher enter the gland mass and send out anastomosing branches.

#### MINUTE STRUCTURE.

*Epidermis of lid, outer surface.*—The epidermal cells have a wavy outline (fig. 3) like that on the ordinary leaves. There are many stomates also like those on leaves (fig. 2). The small glands are very numerous, and consist of 2-8 cells (fig. 8). They resemble the glands of *Sarracenia* figured by Geddes (7). The walls are thicker than those of the ordinary epidermal cells, and are very refractive. The simplest form is rhomboidal, and divided into two by a curved partition across the shorter diameter (fig. 8 *a*). These are comparatively rare, the ordinary type being 6-8-sided, sometimes with a re-entrant angle, with an internal rhomboid divided into two, so that there are six cells (fig. 8 *b*). They average 0.0508 mm. in length. The contents stain very readily with saffranin, and the walls also take the stain. Sometimes, however, the latter remain unstained, and from their strong refractile powers, contrast brilliantly with the stained contents. The stiff hairs stand on raised papillæ formed by two circles of pentagonal cells radiating from the base of the hairs, the cells of the outer circle being larger. The epidermis on the areolæ of the lid is similar to that on the rest of the surface; no hairs emerge here.

*Epidermis: inner surface of lid.*—In surface view the cells are roughly hexagonal, with the greater length lying along the lid. The epidermis pouches downwards and backwards (that is, towards the hinge) in each cell, so that the apex or point overlies the base of the next cell, as the scales on a fish overlap (fig. 9), and from the base fine lines converge to the point. In section the cells show as teeth pointing backward (fig. 10) and becoming longer as the cells are nearer the insertion. These projections continue from the lid down the inner collar, becoming longer till they reach their greatest length at the reflection of the ledge

into the pitcher walls. The small glands already described occur plentifully here, and invariably stain in all parts.

*Mesophyll of lid.*—Beneath the outer surface there is a layer of deeply-staining cells, corresponding to the palisade-tissue of the ordinary leaf, containing chlorophyll, rounded in shape, but with their greater length lying parallel to the surface. They lie closely, and have no intercellular spaces. These deeply-staining cells also surround the vascular bundles. The cells lying under this layer are rounded in form, but longer and larger than the outer cells; and have large intercellular spaces. They take the place of the spongy tissue of the ordinary leaf. They contain little or no chlorophyll and do not stain much. Their walls are thin and sometimes pitted. Under the inner lid epidermis there is a layer of large straight-sided cells with hemispherical bases; these also stain faintly. In the areolæ the cells beneath the outer surface are also of this type. All the mesophyll cells contain starch. There is a considerable amount of vascular tissue with spiral thickenings all through the mesophyll. Blind endings occur here and there under the deeply-staining layer beneath the outer surface; they are thin-walled and have very loose spiral thickenings.

*Body of pitcher: epidermis of outer surface.*—The cells are irregular in shape, and sometimes slightly crenate. The surface presents many small elevations which have a stomate at the top (fig. 15).

*Corrugated rim.*—The epidermis consists of six-sided cells, at least twice as long as broad, the length running along the tooth. Scattered about among them are many of the small glands already described. Beneath the overhanging curved point of the tooth the cells become shorter and gradually change into the imbricated form occurring on the under side of the lid, and their free points lengthen as they near the inner base of the teeth where these join the ledge, till just at the junction they are decided short hairs pointing outward and downward, and they continue down the ledge. At the base of the teeth the hairs reach a length of 0.0381 mm.

*Mesophyll*.—Beneath the epidermis is a layer (4-5 cells thick) of deeply-staining cells, containing much chlorophyll. This layer contains few intercellular spaces, but there are small cavities under each gland similar to those under each stoma. Beneath this layer there is an open network of cells which contain few chlorophyll granules, and stain lightly. This layer is similar to that in the lid, and indeed in the middle layer of all parts of the pitcher. Vascular bundles are very plentiful all through the rim, but are most plentiful in the outer dense layer under the epidermis, where also blind terminations occur, sometimes near glands. After close examination of many preparations, however, I am unable to say that they bear any constant relation to the glands. In the loose interior tissue, wherever the vessels occur, they are surrounded by a sheath of the dense tissue mentioned above as lying under the epidermis. Starch is found plentifully in these cells, and also, but less plentifully, in the middle layer. The substance of the teeth, like that of the lid, and of the pitcher body, is evidently actively assimilative.

*Epidermis of collar*.—This is of the same character as that on interior of lid, but the conical hairs are longer, reaching their greatest length at the interior angle where the collar joins the interior surface. Each cell has a very distinct nucleus. There are no glands, and yet the surface seems attractive to insects, as they stay on it and lick it for a long time.

*Mesophyll of collar*.—The surface view just under the epidermis shows regular hexagonal cells of large size, but none of the granular deeply-staining cells of the corrugated roll. The walls are thin, and the cells gradually pass into the loose network of cells with little chlorophyll and a little starch. Forking vascular bundles are found here, which terminate in loosely spiral blind endings. Here also the vessels are invested with a sheath of dense tissue. The mesophyll is so open that it can be seen to be spongy with the naked eye.

*Interior of pitcher : upper glandular surface*.—The whole of the interior of the pitcher is very smooth and glossy, and as Prof.

Dickson has pointed out (4), when fractured, usually rolls back. The epidermal cells are crenate in surface view. In section, the sides are straight, but the bottom of each cell is hemispherical. The side walls are often pitted—the pits narrow elliptical with the long axis perpendicular to surface of epidermis. The mesophyll cells are rounded in outline, and the cells immediately under the interior epidermis have long narrow pits. The cells under the exterior epidermis are of the deeply-staining variety. This description applies to the mesophyll of all parts of the pitcher.

The glands of this region are of two kinds—(1) Glands like those of the external surface, with few cells, but rather large on the whole. Their sides are straight, so that the glands are roughly cylindrical. (2) Spherical glands resembling those of the lateral gland patches, but smaller. They consist of a large number of rounded cells, 12-20 in number, showing in surface view; and the mass is enclosed by a sheath of flattened cells. Their average size is 0.03 mm. Intermediate forms between the cylindrical and spherical forms occur. The glands are very plentiful, and, so far as I can make out, are not directly connected with vessels, being usually situated between the meshes of the venation.

*Lateral gland patches.*—These are designated by Prof. Dickson the lateral coloured patches. Their position has already been described.

*Epidermis.*—This is composed of crenate cells in all respects like those of preceding region. The glands are spherical (fig. 13), and they are similar to those described for the glandular surface, except that they are much larger—0.1016 mm. Sometimes two are so close together that they fuse and form an elliptical mass. They are most plentiful on the anterior edge of the patches. In some but not all the specimens I examined, the walls of the inner cells of the glands were pitted. The surrounding mesophyll cells stain very deeply, and there is usually much starch present. At the anterior point of the gland mass, where it runs into the ordinary surface, there occur some cells which

are very puzzling. They are remarkably like stomates (fig. 14), but there is not always an opening between the guard cells as shown in figure. In fact, that part stains more readily than the two guard (?) cells.

*Glandular surface.*—This covers the part of the pitcher occupied by the fluid. It is glossy, and the cells resemble in all respects those of the glandular surface, except that there are no glands at all.

*Development of the Pitchers.*—In the very young pitchers, the wings and lid are the most prominent features. The body of the pitcher is very small, and the wings and lid are in consequence all close together, and as they are densely covered with the stiff silvery hairs, the pitcher has the appearance of a little vegetable porcupine rolled up, with its quills standing on end. In this stage—about 2.5 mm. long—if cut open longitudinally, a very small cavity only is seen. There is no sign of the lateral gland patch, and the collar shows a slight thickening. The top edge of the anterior wing overlaps the lid (fig. 11) so that it looks as if the lid and pitcher were joined there; and the lateral wings cover the lid's edge in the same way. In a later stage (6 mm. long) the lid is clasped as before by the wings; the collar shows distinctly, but has no free downward produced edge. There is no sign of the gland patch (fig. 11). In the third stage examined (1 cm. long) the lid is still held by the wing in front, but is free from the lateral wings. It is still closely adpressed to the rim. The collar is beginning to form a free edge, and on the rim the teeth are formed. The gland patch is seen as a thickening of the pitcher wall in that region, and a similar thickening indicates the course of the main vascular bundles. In the later stages, by the growth of the tissue between the wings, the pitcher begins to assume its characteristic form. The first sign of coloration appears on the teeth of the rim, which turn a warm brown; then a crimson line appears on the down-hanging edge of the collar, and on the anterior edge, where the glands are most numerous, of the lateral gland patch.

*Variations of Pitchers.*—The size is variable. I have, on cultivated plants, pitchers only 8 mm. in length with the lid open and insects captured, and a small amount of liquid present. Sometimes the corrugated rim is quite smooth, with only 3 to 5 narrow teeth standing straight up, instead of overhanging the edge of the pitcher (fig. 17).

*Contents of Pitchers.*—The mature pitchers contain liquid up to the lower edge of the glandular surface. The quantity naturally varies with the size of the pitcher. Those measured contained 5, 3.2 and 2.35 ccm. I regret that a quantity collected for analysis was lost by leakage. Lawson Tate gives an account of the digestive principle in *Cephalotus* (8), but I have not been able to see his paper. The liquid is greenish-black in colour from the large quantity of animal remains contained in it, but occasionally one finds a pitcher with only a few victims, and then it is quite clear. Among the débris in the pitchers, I recognised wings of various insects, legs, chitinous plates from thorax and abdomen, balancers of mosquitoes, scales of moths, the claws of a chelifer, living larvæ of a fly, and large numbers of unicellular algæ, consisting of a green cell with a gelatinous envelope; it is probably *Protococcus*, and certainly lives and multiplies in the liquid.

While watching some plants in their native habitat, we noticed flies hovering around the pitchers and occasionally entering them. One of these I captured. Mr. Froggatt informs me it is one of the Tabanidæ. It had the appearance and blood-sucking habits of the ordinary March-fly of New South Wales. It is possible that the larvæ found in the liquid are those of this insect, and that the individuals we saw entering it were intent upon depositing their eggs in the mass of digesting or decomposing insects inside. In any case, the living larvæ are an example of one of those cases, not of symbiosis, but of one organism taking advantage of the conditions created by another for its own benefit. There are many examples of this among insectivorous plants. Geddes (9) mentions an American flesh-fly which lays its eggs on the rim of *Sarracenia* pitchers, and the larvæ when hatched make



their way down into the decomposing mass below, live there, and finally make their way underground to pass the chrysalis stage. Associated with the plant is a bird which slits up the pitchers in search of the larvæ.

In Borneo (10) a spider lines the upper part (the conductive or slippery part) of *Nepenthes* pitchers with a thin web, to give it foot-hold, and there lies in wait for visitors. If disturbed the spider dives into the liquid. We have a parallel case in New South Wales in a bug which lives on *Drosera binata*, and feeds on the insects captured by the sticky tentacles.

At the same time that we observed the flies, we saw a frog, alarmed by our movements, dive wildly into the nearest pitcher, where he was able to hide his head and shoulders.

*Purposes of Structure.*—It is rather a hazardous matter to attempt to account for all the structures of the pitcher, but some are such manifest adaptations that I may venture to point them out. The glands on the outer surface certainly secrete a fluid, and although I have not been able to detect any taste in it, yet I think we are justified in concluding that it is attractive to insects, as they certainly visit and lick the exterior of pitchers. The colours have been supposed to attract as flowers do, but I think this is unlikely, as green mature pitchers had just as large a number of victims as the brightly coloured ones. Indeed, I think the coloration, as in leaves, is a sign of the failure of the vital powers of the pitchers.

In *Nepenthes*, *Sarracenia* and other genera, the wings have been described as staircases leading to the little parlour, and in confirmation of this, it is said that some species of *Nepenthes* which, when young, have short-stalked pitchers resting on the ground, have wings which act as footpaths to creeping insects; while in the mature plants which have the pitchers pendent on the long tips of the laminae, and which depend on flying insects, there are no wings. Probably the wings in *Cephalotus* have some such function, but although I have seen insects on the pitchers, I never saw one on the paths. It may be that they are designed to overlap the edge of

the lid in very young pitchers, and so prevent the ingress of insects when their presence would be undesirable. But again this does not account for their downward production. The lid probably acts as a cover against rain, but it also prevents insects jumping or flying out, and it has been suggested that the transparent windows are designed to cause the insect to fly upwards and be stopped, instead of escaping laterally between the rim and the lid. The recurved teeth and the collar act as the recurved tips in a lobster-pot in preventing exit. The collar acts in the same way as a similar ledge does in a safety ink bottle—it prevents the liquid running out when the pitcher is turned upside down. A pitcher containing the normal amount of fluid lets very little escape when inverted. Insects visiting the pitcher delay a long time licking the surface of the collar before proceeding lower. The fine hairs on the under surface of the lid and on inside of collar are said to prevent insects from crawling up, but they are so very minute that I imagine only very small insects could be stopped by them, unless indeed by getting into the joints of the feet they cause discomfort, or clog their steps. There is no doubt, however, that they facilitate the downward passage of the victim. Below the collar extends the very slippery glandular and eglandular surface, and here the purpose is obvious. Small insects cannot get up it, especially when wet. In some of my plants I found, before the liquid appeared, live harvest-bugs, both crimson and black, and the larger ones could come out at will. Probably many of the victims go into the pitchers as a hiding place.

The purpose of the fluid is a problem worth investigating. Two views are taken: First, that it is merely a culture fluid for bacteria which dissolve or decompose the captives, and so render them available as food for the plant. The pepsin which has been detected in the liquid of some pitchers is said to be derived from the bacteria. In this case there would be a true instance of symbiosis between a high plant and a very low one (11, 12, 13). But this view has been ably combated by Vines (14), whose experiments, made under conditions excluding the action of

bacteria, showed that true digestion, caused by a digestive ferment, took place. And he has also shown that the digestive principle, which is found in various organs of very many plants, is trypsin or some allied ferment. I regret that I have been unable to experiment in this direction, from the difficulty of procuring enough of the fluid, but I hope, as my cultivated plants increase, to be able to do so, and communicate the results in another paper.

There is no doubt that the liquid contains azerin or some similar principle, as the insects falling into the fluid were immediately wetted through, and drowned.

The plants would certainly repay close observation by any one resident in their native locality, and if I am correct in my surmise that they are becoming extinct, it is to be hoped that some one will take up the study before it is too late. I think the trustees of one of our great national parks might well try the experiment of getting some plants and placing them in some of the swampy places with a view to acclimatisation. The swamps occurring in places in the National Park at Waterfall are of exactly the same character as the swamp at Albany where they grow.

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#### REFERENCES TO LITERATURE.

- (1) KERNER & OLIVER.—Natural History of Plants.
- (2) GRANT ALLEN.—The Story of the Plants.
- (3) CURTIS.—Botanical Magazine, tt. 3118 and 3119.
- (4) A. DICKSON.—‘On the Structure of the Pitcher in *Cephalotus follicularis*.’  
Jour. Bot. xvi., 1.
- (5) W. WOOLLS.—Lectures on Vegetable Kingdom, p. 100.
- (6) STRASBURGER.—A Text Book of Botany, 1898. p. 216.
- (7) P. GEDDES.—Encyclopædia Britannica—Art. Insectivorous Plants.
- (8) LAWSON TATE.—Phil. Soc. of Birmingham, 1878.
- (9) P. GEDDES—Chapters in Modern Botany.
- (10) ————Nature, July 21, 1898.
- (11) N. TISCHUTKIN.—Ber. der Deutschen Gesellschaft, 1888.
- (12) ————Acta Horti Petropolitani, vol. xii.
- (13) DUBOIS.—Comptes Rendus, 1890.
- (14) S. H. VINES.—Proc. Linn. Soc. London, Oct. 1903.

## EXPLANATION OF PLATES.

## Plate i.

- Fig. 1.—Monstrous ordinary leaf.  
 Fig. 2.—Stoma, ordinary leaf.  
 Fig. 3.—Epidermal cells, surface view, ordinary leaf.  
 Fig. 4.—Outline of pitcher; *a.* anterior wing; *b.* lateral wing; *c.* corrugated rim.  
 Fig. 5.—Hairs from wings; *a.* short hair; *b.* hair with constrictions; *c.* hair with hyphæ and spores.  
 Fig. 6.—Club-shaped, from insertion of lid.  
 Fig. 7.—Diagrammatic section of pitcher; *l.* lid; *cr.* corrugated rim; *cl.* collar; *gls.* glandular surface; *aw.* anterior wing; *egl.* eglandular surface; *glm.* lateral gland-mass.  
 Fig. 8.—Small glands; *a.* two-celled; *b.* six-celled.  
 Fig. 9.—Imbricated cells, interior of lid, surface view.  
 Fig. 10.—Imbricated cells, interior of lid, in section.  
 Fig. 11.—Very young pitcher.  
 Fig. 12.—Section of young pitcher.  
 Fig. 13.—Section of large glands of gland-mass.  
 Fig. 14.—Cells resembling stomata, gland-mass.  
 Fig. 15.—Section of stoma, exterior of pitcher.  
 Fig. 16.—Front view of young pitcher.  
 Fig. 17.—Undeveloped rim of pitcher.

## Plate ii.

- Figs. 18, 19.—Photographs of growing pitchers.  
 Fig. 20.—Photograph of section of pitcher ( $\times 2$ ).